doi 10.4436/jass.90008

e-pub ahead of print

JASs Invited Reviews

Journal of Anthropological Sciences

Vol. 90 (2012), pp. 1-22

The frontal bone in the genus *Homo*: a survey of functional and phylogenetic sources of variation

Sheela Athreya

Department of Anthropology, Texas A&M University, MS 4352 TAMU, College Station, TX 77843, USA
e-mail: athreya@tamu.edu

Summary - *The frontal bone is a useful aspect of the craniofacial skeleton to study in physical anthropology because it contains several characters considered to be important for both population- and species-level distinctions. These include forehead (frontal squama) inclination and supraorbital morphology. Because it lies at the interface between the anterior neurocranium and the upper face, it is also informative about the evolution of both of these regions of the skull. Previous research on frontal bone morphology can be grouped into two broad categories. One set of studies explored the relationship between craniofacial structure and function in an attempt to explain biological sources of variation in the torus development of various extant primate species, including modern humans. The second group of studies examined geographical and temporal patterns of variation in frontal morphology to make inferences about the phylogenetic relationship relationships among fossil hominin populations in the Pleistocene. This paper offers a review of both phylogenetic and functional studies of variation in frontal bone morphology, and synthesizes them to offer a comprehensive understanding of what the frontal bone can tell us about bio-behavioral and evolutionary differences both among extant and extinct members of the genus* Homo.

Keywords - *Craniofacial variation, Browridge, Supraorbital torus, Pleistocene* Homo.

Introduction

Since the earliest days of paleoanthropology, several features on the frontal bone have been recognized as distinctive among Pleistocene hominins. Even before the 1859 publication of Darwin's *On the Origin of Species*, natural historians were describing fossilized remains of what are now known to be early humans from sites such as Engis in Belgium, Forbes' Quarry, Gibraltar and the Feldhofer Cave in the Neander Valley, Germany. Despite not knowing their exact relationship to modern *Homo sapiens*, scientists regularly commented upon the notable morphology of the frontal bone as a distinctive feature of these specimens [Schmerling, 1833; Busk, 1861; Schaafhausen, 1861 (1858); Huxley, 1863; Lyell, 1863].

After the paradigm shift that took place with the publication of Darwin's work, researchers began searching for evidence of humans in the larger picture of evolutionary change in the natural world. At that time, certain aspects of the frontal bone—in particular the browridge—shaped their notion of archaic human morphology. For example, of the four defining traits of *Homo erectus*, first discovered in 1891 by Dubois (1896), three were located on the frontal bone (Weidenreich, 1941, 1947). Weidenreich (1947) also considered the frontal to be distinctive between Middle and Late Pleistocene archaic *Homo*, in particular Neandertals. Neandertals, as the first hominins to be recognized as human ancestors, were subjected to extensive analyses in which their frontal bone morphology was a central point of discussion regarding their taxonomy, biology and behavior [Busk, 1861; Schaafhausen, 1861 (1858); Blake, 1864; King, 1864; Cunningham, 1908; Keith, 1919; Vallois, 1954; Boule & Vallois, 1957].

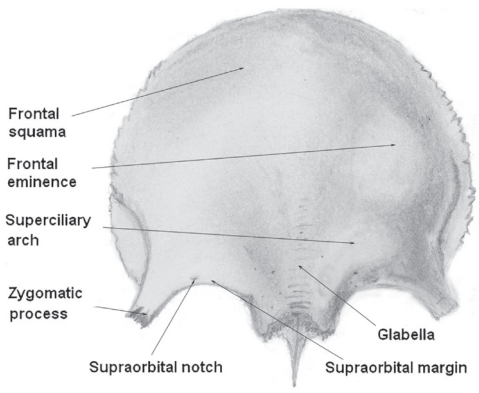

Fig. 1 - External anatomy of the frontal bone.

Yet, despite the long importance that frontal bone morphology has had in defining archaic *Homo*, its sources of variation remained largely unknown throughout the 20th century, and an actual quantitative assessment of the differences among specific groups of Pleistocene hominins has been elusive. Descriptions of regional or species-level differences were primarily subjective. This bone's irregular shape and the absence of a significant number of craniometric landmarks on it made morphometric analyses difficult until the recent advent of curve-fitting and three-dimensional semi-landmark techniques. In addition, because it lies at the interface between the neurocranial and facial skeletons, the question of the role of functional morphology in shaping the frontal bone, particularly the browridge, has been divided into theories regarding the influence of brain growth vs. mastication. In this review I offer a comprehensive discussion of studies that have sought to identify the sources of variation in frontal bone morphology throughout the Pleistocene. I also describe patterns of variation among Pleistocene groups to detail not just why but how the frontal bone varies in our genus.

The anatomy of the frontal bone

The frontal bone lies at the interface between the neurocranium and splanchnocranium (facial skeleton), with the neurocranial part forming the superior portion of the bone and the facial part forming the inferior portion. The browridge, or supraorbital torus, is part of the facial portion. It is typically further subdivided and will be described in more detail below. Embryologically, this bone derives from a neural crest origin. It ossifies from two separate centers above each orbit *in utero*, and at birth these centers remain separate such that the frontal is comprised of two unjoined bones. A cartilageneous membrane, or fontanelle, lies between them to allow a certain degree of flexibility and elasticity of the skull when it is passing through the birth canal, and also to accommodate the rapid brain growth of the neonate. This anterior or frontal fontanelle usually disappears by age 2, when the two separate bones of the frontal fully ossify. Their union is then marked by a metopic suture, also known as the frontal suture. By the sixth year, the metopic suture is obliterated externally although in rare cases it persists into adulthood, usually without association with any pathology.

The external surface of the superior portion of the frontal bone is vertical in orientation in anatomically modern humans, and comprises the forehead or frontal squama (Fig. 1). Even in archaic *Homo* with sloping frontals, the squama is more or less vertically oriented with respect to the Frankfurt Horizontal (FH) and thus can be still be described as the vertical portion of the frontal. The regions immediately lateral to the metopic suture are the locations of the original centers of ossification, and in some modern and archaic humans these regions appear raised or rounded. When such morphology is present they are termed *frontal eminences* or *bosses*. The temporal lines are also present on the ectocranial surface of the superior portion of the frontal bone, marking the supero-anterior extent of the attachment of the temporalis muscle and its fascia.

Internally, the superior portion of the frontal is characterized by several meningeal grooves as well as a midline or frontal crest. The latter is the point of attachment of the cerebral falx, a strong membranous portion of the dura mater between the right and left hemispheres of the brain. The posterior portion of the frontal crest ends in the *foramen caecum*

where the frontal articulates with the ethmoid bone. This foramen transmits veins connecting the superior sagittal sinus to the nasal region.

The external surface of the inferior (facial) portion of the bone is shaped primarily by the complex morphology of the supraorbital region, particularly in archaic *Homo*. When this region is characterized by a continuous ridge of bone above the orbits, it is also known as a supraorbital torus. Russell (1985) and Lieberman (2000) define three subregions of the torus (Fig. 2): 1) the glabellar region, located along the midline of the frontal bone above the frontonasal suture and directly between the brows, 2) the supraciliary region, located just above the medial portion of each orbit (adjacent to the glabellar region) and 3) the supraorbital region, i.e., the lateral portion of the bony region just above each orbit. In addition, the frontozygomatic process that adjoins the ascending frontal process of the zygomatic bone occasionally forms part of the supraorbital torus as well. When it is highly developed, it is known as the supraorbital trigone and is present even in some modern humans (Cunningham, 1908; Weidenreich, 1951).

Two sulci are occasionally present on the supraorbital portion of the frontal as well. The glabellar region, while conventionally defined as the most anterior part of the frontal above the frontonasal suture (White & Folkens, 2000), is occasionally characterized by either a complete lack of prominence (Howells, 1973) or even a depression in this region (Weidenreich, 1951). When a depression is present, this is sometimes referred to as a glabellar sulcus. The term supratoral sulcus refers to the depression that occurs, particularly in late archaic *Homo*, at the juncture between the supraorbital torus and the frontal squama (Weidenreich, 1951). In modern humans, the term supraorbital sulcus refers to a discontinuity or groove between the supraciliary arch and supraorbital arches, typically located along the bony portion above the middle of each orbit (Russell, 1985).

All members of the genus *Homo* possess a projecting supraorbital torus with the exception of modern *H. sapiens*. Specifically this is referring to a

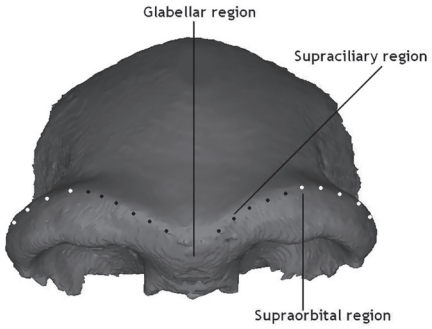

Fig. 2 - Subregions of the supraorbital torus.

projecting browridge that is at minimum continuous over each orbit and has some vertical thickness. Such a structure is present in all archaic hominins and takes different forms over the orbits (arched *vs.* straight), may or may not be interrupted by a swelling or depression at glabella, and varies in thickness supero-inferiorly. In contrast, modern human browridge development varies by population and, if present, is usually characterized mainly by pronounced supraciliary arches. If a lateral supraorbital arch is present, it is always interrupted by a supraorbital sulcus, thus precluding *H. sapiens* from having a proper supraorbital torus. Instead, the entire supraorbital region in modern humans is occasionally referred to as the superciliary arch, not to be confused with the more medially situated supraciliary swelling defined above. Modern humans are characterized by a more vertical forehead or frontal squama and more retrognathic faces overall, which then eliminates the supratoral sulcus.

Internally, the inferior portion of the frontal bone is occasionally characterized by a frontal sinus although its presence and form are highly variable in fossil and modern humans (Bookstein *et al.*, 1999). While the presence of a frontal sinus is often coincident with a prominent supraorbital torus, several studies have shown that sinus growth is not a driver of supraorbital morphology (Tillier, 1977). Rather, as will be shown below, both appear to be a consequence of differential patterns of growth between the internal and external tables of the frontal bone (Bookstein *et al.*, 1999; Lieberman, 2000).

Previous research on frontal bone morphology can be grouped into two broad categories. Both share a focus mainly (but not exclusively) on the supraorbital region. One group of structural/functional studies provides information on potential ontogenetic/behavioral sources of variation by exploring the relationship between craniofacial structure and function in an attempt to explain sources of variation in torus development among extant primates, including modern humans. The second group of studies examines the geographical and temporal patterns of variation in frontal morphology to make inferences about phylogenetic relationships among fossil hominin populations in the Pleistocene. These two bodies of study are interdependent, because by understanding the possible developmental or behavioral sources of variation, we can then better evaluate the significance of geographic and temporal patterns of variation in this bone within the genus *Homo*.

Biological sources of variation: functional and structural studies

Biomechanical Models

There are two related biomechanical models that seek to explain the presence of a supraorbital torus, and both explore evidence of whether this trait is a structural response to masticatory stress. The first explanation relates deposition of bone in the browridge region to tooth eruption patterns (Endo, 1970; Russell, 1985). The second proposes that strain from the muscles of mastication from either anterior dental loading or strong chewing/biting forces leads to browridge development (Endo, 1970; Oyen *et al.*, 1979b; Russell, 1985; Hilloowala & Trent, 1988). Both will be reviewed in detail here.

Tooth eruption and browridge bone remodeling

The relationship between tooth eruption and bone remodeling in the browridge was initially proposed by Oyen *et al.* (1979a, b) and Russell (1982). Based on research with olive baboons, Oyen *et al.* (1979b) put forth the possibility that cycles of cancellous bone deposition and remodeling of the browridge region were related to alterations in the masticatory system as a consequence of tooth eruption. Russell (1982) tested this model on a population of Native Australians. Comparing different individuals at identical stages of tooth eruption, she found no significant relationship between the two variables. In other words, she was not able to confirm the hypothesis that bone is more likely to be deposited in the supraorbital region during tooth eruption in her human sample.

Masticatory stress from anterior dental loading

The idea that the browridge develops in response to biomechanical forces produced during biting—in particular masseter muscle action during anterior dental loading—was first put forth by Endo (1970) and led to an extensive series of experimental studies. In order to test the effects of masticatory stress on the supraorbital region Russell (1985) modeled the torus as a beam and the masseter and temporalis muscles as bending forces on the lateral aspects of the beam. From there, she developed predictions on the basis of statics theory, which is essentially the study of mechanical stress (i.e., bending or other kinds of force, torque, or movement) on a static system (i.e. one that is in equilibrium in some way). She proposed that the development of the supraorbital torus was a function of bending stresses on the "beam" (i.e., the browridge) by the masseter muscle due to anterior dental loading. She took into consideration the degree of prognathism and slope of the forehead (craniofacial angle) when calculating the forces placed on this region. The rationale was that the moment arm of masticatory muscle force was affected by this orientation.

Using the mathematical formulas developed for this model by Endo (1970), Russell found a significant relationship between craniofacial angle and development of the supraciliary arches. Her results implied that the angle of slope of the face and forehead affected the orientation of the masseter and temporalis muscles, inducing greater strain on the supraorbital

bone and causing increased bone deposition and remodeling on the torus. She interpreted this as a result of severe masticatory and paramasticatory stresses, particularly those due to incision.

Picq and Hylander reviewed both Endo's and Russell's work, and found several limitations to their models (Picq & Hylander, 1989; Hylander *et al.*, 1991). These authors challenged the proposition that the specific torus area can be modeled as a beam. If sinuses are present, this region can be hollow, and hollow beams have different static properties. Additionally, this structure has variable topography such as a pronounced glabellar region, or a supraorbital sulcus, in different individuals. This variability could influence the browridge's ability to resist force. Also, these authors failed to confirm that this region of the frontal bone actually underwent the magnitude of strain during anterior loading that served as the primary explanation for Russell's results.

Using *in vivo* bone strain studies on *Macaca fascicularis* and *Papio anubis* during mastication, Hylander *et al.* (1991) tested the masticatory stress hypothesis. Their research confirmed that the supraorbital region was bent in the frontal plane but not the sagittal, as Russell's model predicted. They also found that this bending did not necessarily occur more during incision than mastication, nor did the recorded levels of strain increase in more prognathic subjects. The overall levels of strain throughout this region were low in both gorilla and humans skulls relative to other parts of the face, suggesting that the presence of a pronounced browridge was more complex *vs*. simply serving a functional role of countering masticatory loads.

To date, the functional/behavioral models relating masticatory stress or tooth eruption to browridge morphology do not provide sufficient evidence for explaining frontal bone variation among or within groups. In fact, they seem to show that morphological variation in the frontal bone is *not* due to behavioral stresses. While this does not answer questions about inheritance or adaptive significance, it does imply that the complex biological system that shapes this region of the skull is not subject to serious behavioral remodeling through masticatory stress. Therefore, interpreting this morphology in a phylogeographic context is still a valid and potentially useful approach to understanding overall patterns of hominin craniofacial variation.

Cranial robusticity and cortical thickness models

Another line of research on frontal bone morphology proposes that overall robusticity, possibly from excessive deposition of cortical bone related to exercise or other systemic factors, may explain the morphology of this bone, particularly in hominins (Hublin, 1987; Lahr & Wright, 1996; Lieberman, 1996). The notion that the browridge was the product of an overall systemic response was first introduced by Keith (1919), who suggested that the Neandertal supraorbital torus was a result of the endocrine disorder acromegaly. The absence of other skeletal evidence for acromegaly, as well as the universality of the prominent brow among archaic *Homo* makes this an impossibility, but Keith did introduce the idea that a prominent browridge was not a localized response to a particular stress, but rather the result of a system-wide process.

One hypothesis in this vein that also relates back to Oyen's research on bone deposition in the supraorbital region comes from Lieberman's experimental work (Lieberman, 1996). He suggests that systemic cortical robustness can be related to the effects of exercise, particularly during periods of skeletal maturation. Lieberman showed through experimental studies that the vaults of exercised animals (the miniature domestic pig, *Sus scrofa*, and the common nine-banded armadillo, *Dasypus novemcinctus*) have an average thickness that is 28% greater than the control animals. He concluded that this result was almost entirely due to increased lamellar deposition on the outer table of the cranial vault, as Oyen had observed. He suggested that these results could be due to the increased production of growth hormone, stimulated by elevated activity levels.

This research has the potential to confirm the hypothesis by researchers such as Hublin (1987) that well-developed browridges are a product of

overall increased cranial robusticity due to the hormonal factors suggested by Lieberman. That is, if cortical thickness is a reflection of increased endocrine activity, as proposed by Lieberman, then it may also be correlated with general robusticity, as in acromegalics. One can then make the connection that higher activity levels are related to the development of robust cranial superstructures such as keel development and torus size. Thus, Hublin's argument that connects frontal bone morphological variation to robusticity would hold true, and the source would be a systemic response to behavioral stressors.

A related question is the extent to which frontal sinuses contribute to browridge projection. Moss & Young (1960) have shown that as frontal bone thickness increases, pneumatization is more likely to occur. The direction of this correlation has not been definitively proven. Larger sinuses could be the result of increased deposition of cortical bone in the supraorbital area, which would lead to overall thickening of the torus and, secondarily, to the development of sinuses. Or, a scenario conventionally considered to be less likely is that an enlargement of the sinuses leads to greater supraorbital torus development. However, detailed studies have consistently demonstrated that there is no evidence for the latter (Tillier, 1977; Seidler *et al.*, 1997; Bookstein *et al.*, 1999). The formation or form of the frontal sinuses does not have any direct influence on the form of the external browridge.

Craniofacial architecture models

A number of studies on frontal bone morphology have framed variation as a product of spatial relationships between the anterior neurocranium and face, with changes in this bone being driven by the expansion of the brain and the changing structure of the cranium (Weidenreich, 1941; Moss & Young, 1960; Shea, 1986; Enlow & Hans, 1996). Similar ideas are also embodied in discussions of encephalization, which significantly increased during the Middle Pleistocene (Leigh, 1992; Ruff *et al.*, 1997). This idea has its roots in the late 19th and early 20th century. Following the discovery of the original Neandertal fossil in Germany, Schwalbe [1899, 1901, 1906 (in Cunningham, 1908); Weidenreich, 1941] immediately recognized the distinctiveness of the frontal bone in pre-modern *Homo*. His observations inspired further study into the etiology of the torus by his student, Weidenreich (1941), as well as Cunningham (1908) in the first half of the 20th century. Most of this early research focused on the relationship between the brain and the orbits, particularly in light of the expansion of the cerebral cortex. A discussion of the expansion of the anterior brain and its influence on frontal bone morphology is discussed in further detail below. Here, the focus is on how the work of these scientists ultimately formed the basis for the spatial explanation for the degree of development of the supraorbital torus.

According to the spatial model, changes in the structural relationship between the orbits and anterior neurocranium are the primary determinants of frontal bone morphology (Moss & Young, 1960). In species with large prognathic faces, the orbits and face are displaced anteriorly relative to the braincase, calling for a "horizontal space filler" of bone, so to speak--namely, the supraorbital torus. Related to this phenomenon is a progressive flattening of the forehead. Proponents of this model also believe that the torus serves to strengthen and protect that region of the head in the absence of other structural reinforcements (e.g., Hylander *et al.*, 1991).

Shea (1985, 1986) and Ravosa (1988, 1991) have separately pursued this structural explanation through analyses of African primates. Shea's work focused on studies of African ape and orangutan skulls. The latter Asian species served as a comparison because it lacks prominent toral development. Using angular measurements, Shea assessed the relationship between the orbital axes of orientation, maxillary plane, and cranial base. He demonstrated that the splanchnocranium in *Pongo*, while maintaining the same shape as the African apes, is positioned differently: it is dorsally inclined relative to the braincase. Shea's work also addressed the fact that this trait develops ontogenetically. In African apes, the percentage of the orbital roof that is overlain

by the contents of the anterior neurocranium gradually decreases during growth due to the fact that the face is displaced anteriorly relative to the braincase. The result is to position the orbits further from the anterior neurocranium, thus creating the need for a bar of bone to fill in the intermediary space. Looked at another way, the proximal relationship between the orbital cavities and braincase in orangutans *eliminates* the need for a bony torus.

Ravosa (1988, 1991) has also pursued an understanding of the relationship between the orbits and the development of a supraorbital torus. His work specifically focuses on the relationship between the orbital and neural (frontal lobe) tissue. His results suggest that this relationship is not a "prime mover" in determining torus morphology. Rather, Ravosa's research suggests that face and skull size are the most significant determinants of torus development. In particular, he was one of the first to demonstrate quantitatively, across several primate genera, that facial size and orientation were significant determinants of the antero-posterior dimensions of the browridge.

May & Sheffer (1999) sought an understanding of the growth trajectories of various regions of the upper facial skeleton of different hominoid and fossil hominin species. Studying changes and differences in the position of various midline craniometric landmarks, they found a variety of sources of upper facial projection in their study species. While frontal bone thickness explains the projection of robust australopithecine faces, the upper face of *Homo* was found to be projecting due to the length of the anterior cranial fossa.

Lieberman (2000) has provided one of the most comprehensive reviews of sources of variation in frontal bone morphology. In particular he assessed the ontogenetic and architectural basis for a prominent supraorbital torus in archaic *Homo*. He also compared supraorbital morphology in early hominins to that of anatomically modern humans. He ultimately found that the model first proposed by Weidenreich in 1941 was the most successful at explaining browridge formation. In essence, prominent browridges are a byproduct of upper facial projection, which occurs due to the differential patterns of development of the inner vs. the outer tables of the frontal bone (which, he notes, are part of the neurocranium and face, respectively) (Lieberman, 2000). He concluded that browridge formation is not affected by *in vivo* response to masticatory strain, nor is simply an allometric consequence of cranial size. While allometric differences do explain an element of browridge morphology, they cannot entirely explain variation in torus robusticity. Rather, allometric differences in the upper face and projection secondarily affect browridge morphology, including influencing sexual dimorphism in modern humans (Rosas & Bastir, 2002).

Phylogenetic analyses of the genus *Homo* based on frontal bone morphology

Questions about the phylogenetic significance of frontal bone variation within the genus *Homo* have been present since the beginning of paleoanthropology. Most of these studies consider supraorbital torus morphology in particular to be distinctive, even diagnostic, between African (*H. ergaster)* and Asian *H. erectus,* Neandertals, and modern humans (Cunningham, 1908; Weidenreich, 1951; Lahr & Wright, 1996). For example, as stated in the Introduction, the original Neandertal fossil was immediately considered notable due in large part to its unusual browridges (Boule & Vallois, 1957; Trinkaus & Shipman, 1992). Weidenreich (1947) also considered this region to be important in the assessment of the relationship of Middle Pleistocene *Homo* to Neandertals. Since that time, the morphology of the frontal bone has become central to the definition of Neandertals. They are said to be characterized prominent browridges arching laterally over each orbit but nonetheless forming a continuous bar of bone across the upper face with a glabellar depression separating each arch (Le Gros Clark, 1955; Smith & Ranyard,

1980; Smith *et al.*, 1989), although the glabellar region has also been described as occasionally projecting (Santa Luca, 1978; Rosas *et al.*, 2006). The supratoral sulcus is considered to be more pronounced in the lateral portions of the torus than the medial (glabellar) portion and less pronounced than in *H. erectus*. Together, this frontal morphology is considered distinctive relative to both *H. erectus* and *H. sapiens* (Dubois, 1937; Smith & Ranyard, 1980; Lahr & Wright, 1996).

Similarly, upon its discovery, *Sinanthropus pekinensis* was considered to have four defining traits, two of which were on the frontal bone: supraorbital torus morphology and the configuration of the forehead relative to the torus Weidenreich (1937). Several traits that have subsequently been agreed upon as defining *H. erectus* appear on the frontal bone such as a low frontal with a well-developed supraorbital torus that forms a straight, continuous bar of bone above the orbits when viewed superiorly, a variably present supratoral gutter or sulcus, and a flattened frontal squama (Weidenreich, 1943; Le Gros Clark, 1955; Rightmire, 1990; Antón, 2002). Differences in the frontal have also been used to distinguish the Chinese and Indonesian *H. erectus* specimens, with the latter being described as having a straight continuous bar of bone above the orbits that grades directly into the frontal squama, and the former having a more pronounced sulcus that separates the browridge from a slightly more vertical squama (Weidenreich, 1943; Antón, 2002). However, these differences have been used to illustrate interregional variation in Asian *Homo erectus* rather than to argue for differentiation at the species level.

Several studies have used characters on the frontal bone to support a particular evolutionary model or interpretation of the fossil record. Assessments of variation in this bone have been brought to bear on debates about the meaning of craniofacial differences among African, European and Asian Middle Pleistocene *Homo* as well as the evolutionary relationship between Neandertals and early modern humans (Rightmire, 1985; Spitery, 1985; Stringer, 1985; Bräuer, 1992; Lahr, 1994; Lieberman, 1995; Athreya, 2006). The traits regularly considered to be important and highly variable include: degree of post-orbital constriction, frontal squama angle, bregmatic eminence, frontal keeling, glabellar morphology, supratoral sulcus morphology and size, minimum and maximum frontal breadth, and degree and patterning of supraorbital torus development. These assessments came to variable conclusions about what the observed patterns of frontal bone variation meant vis à vis a particular model of the fate of *H. erectus* or origin of modern humans. Often (although not always) the morphology was minimally quantified and thus open to a great deal of subjective interpretation.

Other historically significant frontal bone studies have focused on this cranial region in phylogenetic assessments of new fossil finds (Boule, 1913; Heim, 1976; Conroy *et al.*, 1978; Stringer *et al.*, 1979; Arsuaga *et al.*, 1997). As with the previous set of studies, for the most part researchers have used a combination of metric and non-metric features on the frontal to build inferences about evolutionary relationships in the Pleistocene. While most of the previous studies were limited to the information that could be obtained from a visual assessment of non-metric traits, or from linear measurements taken between craniometric landmarks, some researchers have attempted to expand their database by including non-landmark based measurements. These are worth reviewing, because they address the inherent limitations that are present in quantifying the complex morphology of the frontal bone. Their results are somewhat consistent, and shed light on the possible phylogenetic significance of variation in this bone among Pleistocene *Homo*.

The first multivariate analyses of various landmark and non-landmark based linear measurements of the supraorbital torus was in 1980s and early 1990s (Smith & Ranyard, 1980; Smith *et al.*, 1989; Simmons, 1990; Simmons *et al.*, 1991). The goal of these studies was to identify evolutionary trends during the later Pleistocene by focusing on morphological changes in one cranial element on the frontal bone. Smith and Raynard (1980) conducted a metric analysis of

supraorbital thickness and projection of a sample of Late Pleistocene archaic and modern humans from Central Europe. They evaluated supero-inferior thickness at the medial, lateral and midorbit portions of the torus along the orbital segments; they also took projection measurements at those points. The results did not find any significant difference between the archaic (Neandertal) and early modern humans in the region. Rather, supraorbital morphology was continuous in form from the early Neandertals (Krapina) through the late Neandertals (Vindija) and early modern humans. They took this as an indication of a general process of transition between Neandertals and early modern humans in this region, a finding that Smith *et al.* (1989) later suggested was a pattern true for all of Europe. This idea has since been substantiated through other craniofacial elements and fossil finds for Central Europe (Trinkaus *et al.*, 2003; Trinkaus & Svoboda, 2006; Trinkaus, 2011) and Southwest Asia (Simmons, 1990; Simmons *et al.*, 1991). The latter research, built on Smith *et al.*'s previous work, was a further quantitative analysis that analyzed both raw and log-shape data to better understand frontal bone patterns of variation. The results showed that, as in Central Europe, the Southwest Asian hominins showed continuity in frontal bone morphology—specifically, between the early modern human Skhul/Qafzeh sample and earlier archaic humans.

Dean's (1993) work was a further innovation in frontal bone morphometrics in that it provided a valuable assessment of Middle Pleistocene hominin cranial morphological differences based on space-curve statistics. He collected three-dimensional digitized outline tracings from the glabellar region, the lateral browridge, temporal line, and coronal suture along with one trait that does not fall on the frontal bone, the superior nuchal line. Dean found that certain aspects of the frontal—namely the glabellar region—were unique for *H. sapiens* relative to archaic *Homo*; other aspects such as the coronal suture region were not distinctive between *H. erectus* and later Middle Pleistocene *Homo*. His work represents an important precedent to subsequent research on the phylogenetic significance of frontal bone variation through the use of 3-D data and the quantification of curves. Ultimately, this study formed a significant part of the basis for the "accretion" model of Neandertal facial form (Dean *et al.*, 1998; Hublin, 1998).

More recently, a study was conducted by Freidline *et al.* (2012) on the fronto-zyogmatic morphology of the Zuttiyeh specimen. The authors used 3-D semi-landmark data and compared Zuttiyeh to a broad sample of Middle Pleistocene *Homo*, Neandertals and early modern humans. They found that Zuttiyeh displayed a generalized archaic frontal and zygomatic morphology, and could thus represent the last common ancestor of Neandertals and modern humans if its geological age was confirmed to pre-date the split between these two lineages. Based on the present estimates of the age, however, which would post-date the split, they proposed that its fronto-zygomatic morphology was more similar to Neandertals and thus it represented an early member of this group.

The extent to which the frontal bone is diagnostic among archaic *Homo*, however, is questionable. Among Middle Pleistocene *Homo*, I found (Athreya, 2006) that the frontal bone was not useful in extrapolating parameters of past population structure or phylogenetic history. I also found (Athreya, 2009) that among archaic members of the genus *Homo*, there are very few traits that distinguish among them. These will be discussed in more detail below, and will show that while the results of Freidline *et al.*'s (2012) study are intriguing and call for further investigation into the patterning of evolutionary change in the Levant (also proposed by Bruner *et al.*, 2004) the evolutionary valence of the fronto-zygomatic region and its ability to reveal broader phylogenetic branching events is questionable.

A study by Bookstein *et al.* (1999) attempted to gain a better understanding of overall frontal bone morphology by analyzing the internal and external aspects of the frontals of 16 modern humans and five mid-Pleistocene hominins using the 3-D morphometric Procrustes analysis. Though their analysis relied upon lateral

radiographs and was thus restricted to a study of the mid-sagittal profile, their research was the first to apply Procrustes analysis to the study of frontal bone evolutionary change in Pleistocene *Homo*. They were attempting to understand the relationship between inner and outer aspects of the frontal bone, and thus their work relates to previously discussed studies seeking to understand sources of variation in frontal bone morphology. Interestingly, they found that while the external morphology of the frontal—namely, the browridge—changed considerably from the Middle to Late Pleistocene, there was actually a great deal of stability in the inner table of the frontal bone. This suggested a comparable stability in frontal lobe morphology over a long period of human evolutionary history. Their study also demonstrated the independence by which the inner and outer aspects of the frontal changed over the course of the Pleistocene (Fig. 3).

Similarly, Seidler *et al.* (1995, 1997) analyzed the human medial sagittal plane using trignonmetric curve-fitting analyses of 50 modern humans as well as four fossil casts to demonstrate the viability of this approach. Later, they used stereolithographically-modeled skulls of two Middle Pleistocene specimens, Kabwe and Petralona, to examine the anterior cranial fossa and the effect of pneumatization in this area on overall cranial morphology. They, like Bookstein *et al.*, found that there was considerable divergence between patterns of variation in the external morphology of the frontal bone vs. the endocranial portion interfacing with the anterior brain. In particular, both studies found that the anterior lobes of the brain were situated behind, vs. above the orbits in the Middle Pleistocene fossils Petralona, Broken Hill, and Sima de los Huesos 5. While the authors were cautious to draw conclusions about what these findings meant in terms of cognitive function, these studies furthered the research on the relationship between paleoneurology and fossil craniofacial morphology. In the subsequent decade, several studies integrated these two fields in order to develop a better understanding of the significance of frontal bone variation for modern human origins.

Similar to Bookstein *et al.*'s (1999) study, Bruner *et al.* (2004) used geometric morphometrics to evaluate variation in midsagittal cranial profiles of a fairly broad sample (n=19) of Pleistocene specimens along with one Pliocene specimen from Sterkfontein. Using Thin Plate Spline and Procrustes analysis, they evaluated the entire midsagittal profile vs. just the frontal. They found a clear separation of the western European Neandertals and anatomically modern *H. sapiens*, with the latter exhibiting frontal enlargement while the former retained plesiomorphic traits in the vault, but derived morphology in the face. Comparable to Simmons *et al.*'s (1991) finding, the status of the Southwest Asian Neandertals was less clear. In addition, as other studies later substantiated, the affinities of Irhoud 1 were also mixed.

Further studies by Bruner & Manzi (2005, 2007) to evaluate the Ceprano specimen yielded interesting results with respect to the architecture of the frontal bone, both endo- and ectocranially, among Middle Pleistocene *Homo*. Their results confirmed the findings of previous studies that among archaic *Homo*, the frontal lobes are posteriorly positioned relative to the orbits instead of resting above them. In addition, they found that there has been a bilateral widening of the frontal lobes among Late Pleistocene (Neandertal and early modern human) populations. Upon further investigation (Bruner, 2007; Bruner & Holloway, 2010), this expansion was confirmed as being due to more than just an overall increase in cranial capacity. Rather, in the Late Pleistocene there appears to have been a proportional increase in the anterior brain in particular. This finding is particularly relevant given Cunningham's (1908) original interpretation of the low frontal profile of Neandertals which he posited was a reflection of their smaller frontal lobes and thus decreased capacity for rational thought relative to modern humans. While Bruner and colleagues (Bruner, 2007; Bruner & Holloway, 2010) do not assert specific outcomes or make phylogenetic inferences based on this reorganization of the architecture of the brain, they do consider its possible implications particularly with respect to neural

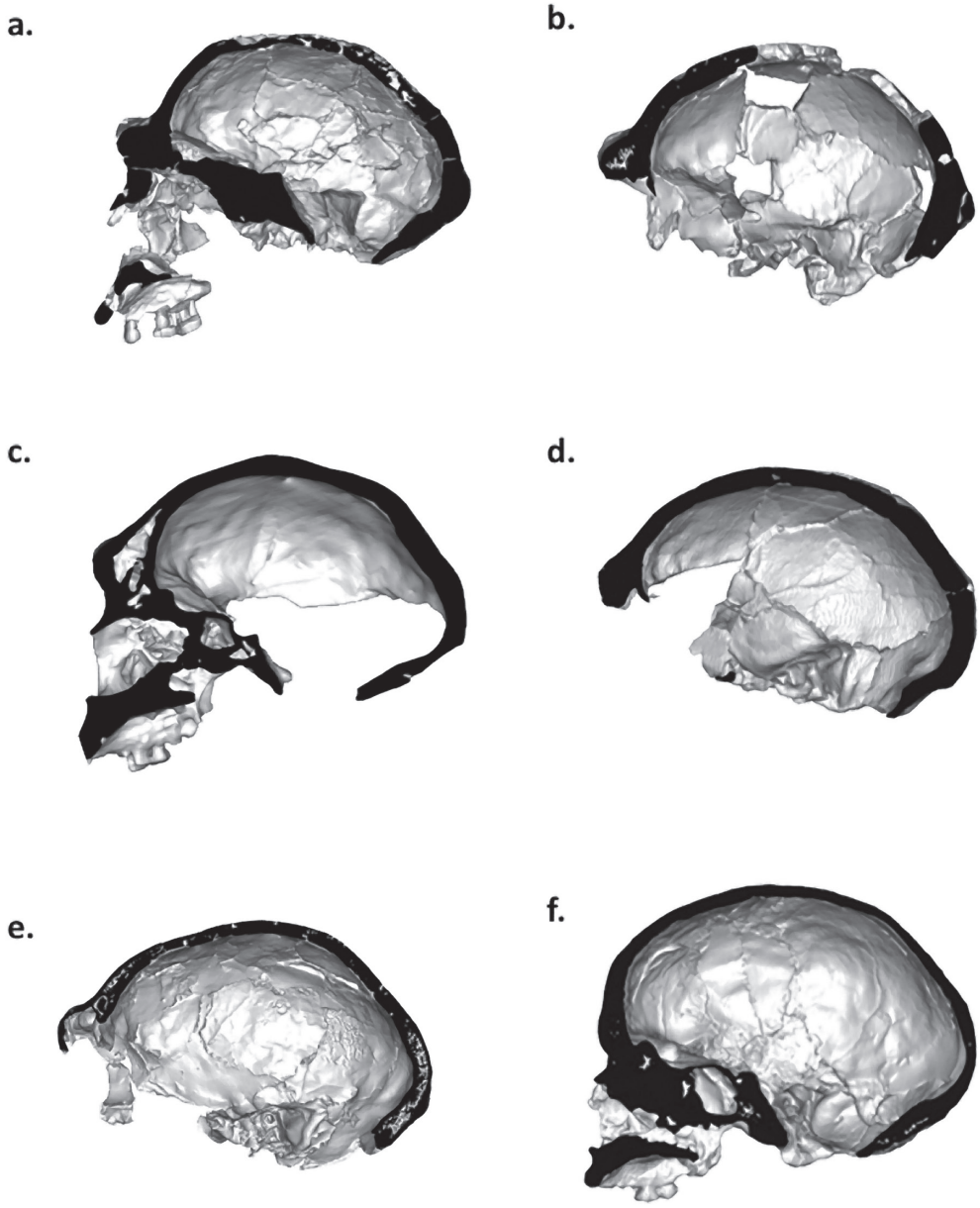

Fig. 3 - Frontal bone inner vs. outer table variation among Pleistocene* Homo *: a) KNM-ER 3733; b) Ceprano; c) Broken Hill; d) Laetoli 18; e) Spy 1; f) Mladeč 1.

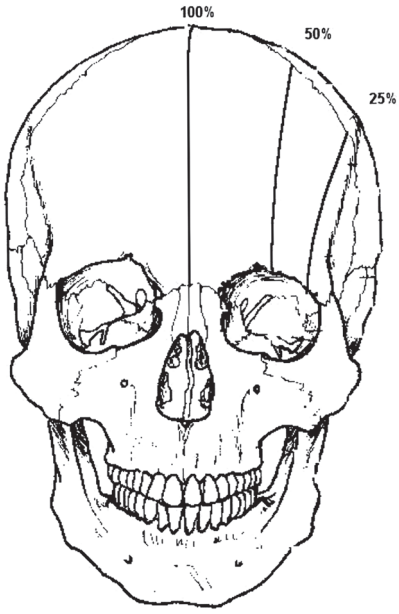

Fig. 4 - Three outlines taken in Athreya's (2006, 2009) study.

functions such as language (particular given the location of Broca's area on the left prefrontal cortex), working memory, and decision processing.

The result of these studies has allowed us to make inferences about the relationship between frontal bone morphological variation and neural functioning in Pleistocene *Homo*. Clearly, based on this research, variation in the ectocranial facial portion of the frontal bone (particularly the browridge) is independent of variation in the endo/neurocranial (squamal) portion. Browridge morphology varies more widely throughout the Pleistocene and while it may be patterned somewhat geographically, it is not related to brain architecture. In contrast, the frontal squama and particularly the endocranial aspect of the frontal bone is relatively stable for several hundred thousand years of evolution, from the Middle to Late Pleistocene. In the Late Pleistocene, we see both a lateral and (with anatomically modern humans) vertical expansion of the frontal bone related to a repositioning of the anterior cerebral cortex above the orbits.

Temporal and regional variation in Pleistocene *Homo* frontal bone morphology

Recently, I conducted a similar study of sagittal profiles of the frontal bone of the largest samples of Pleistocene hominins (n = 55) available, to assess the patterning of variation within and among groups of hominins (Athreya, 2006, 2009). Three outlines were analyzed for this research: the midsagittal profile from nasion to bregma as well as two parasagittal profiles above the medial and lateral sections of the orbit, respectively, extending from the orbital margin to the coronal suture (Fig. 4). These were traced using a modified pantograph, and then digitized and analyzed using Elliptical Fourier Analysis, a curve-fitting morphometric method. The fossil sample ranged from the earliest Pleistocene to the end of the Late Pleistocene (Tab. 1).

Based on the results, certain things can be said about frontal bone variation along temporal and regional lines. The Early Pleistocene sample was significantly different from *H. erectus* (*sensu stricto*) in frontal chord length and frontal subtense or forehead height. In particular, the African early *Homo* were significantly different from the Indonesian *H. erectus* in these two traits in that the latter had longer, more rounded frontals. This is undoubtedly a reflection of the vast temporal difference between the two groups, since the African *H. erectus* date to older than 1.5 million years ago and the Indonesian specimens analyzed here have been dated to the later-Middle Pleistocene (Indriati *et al.*, 2011) or possibly the early-Late Pleistocene (Barstra *et al.*, 1988; Barstra & Basoeki, 1989).

Within the Asian *H. erectus* sample, two of the Ngandong specimens (7 and 11) had the highest values in the sample for glabellar projection (Fig. 5). Originally the Ngandong sample was described as possessing a glabellar depression (Dubois, 1937) and the Zhoukoudian and Trinil/Sangiran specimens were viewed as possessing a glabellar torus (Weidenreich, 1943, 1951). Others have described variability in this

trait within regional samples (Santa Luca, 1980; Stringer, 1984; Antón, 2003). This morphology is significant because, relative to the Late Pleistocene groups in the study, glabellar projection was diagnostic for *H. erectus,* which had on average a more prominent glabellar region than other groups.

When the Chinese and Indonesian *H. erectus* samples were compared to each other, they were not statistically significant, nor were the patterns of separation discrete enough to characterize the fossils from one region to the exclusion of the other. However, when comparing each Asian sample to the African *H. erectus*, I found that the Chinese *H. erectus* were never significantly different from the Early Pleistocene Africans, but the Indonesians were. As previously stated, this was true for frontal subtense height and frontal chord. They were also significant different from AMHS in the projection of the lateral browridge. Previous studies that examined a wider range of morphology than was captured here (Weidenreich, 1951; Antón, 2002, 2003) have described certain differences. However for supraorbital torus projection, frontal chord, and frontal curvature, the interregional differences in Asian *H. erectus* are not significant but the fossils from China vs. Indonesia do show differential affinity to other groups.

The non *H. erectus* fossils from the Middle Pleistocene, often referred to as *H. heidelbergensis*, have been evaluated for systematic regional differences in frontal bone morphology and none were found (Athreya, 2006). This is consistent with studies of the endocranial aspects of Middle Pleistocene frontal bones, which have similarly suggested a common, general archaic pattern of frontal bone morphology that does not appear to exhibit regional distinctions (Bookstein *et al.*, 1999; Prossinger *et al.*, 2003; Bruner & Manzi, 2005). In my (Athreya, 2009) analysis, Middle Pleistocene *Homo* is morphologically intermediate between the *H. erectus* and Neandertal samples in most aspects of frontal bone morphology. However, there appears to be a specific shape associated with Middle Pleistocene *Homo* lateral frontal bone morphology: the parasagittal profiles (taken above the mid-orbit and the lateral portion of the orbit) were significantly different in both raw and size-standardized analyses from

Tab. 1 - Sample and fossil classifications from Athreya (2009).

SPECIMEN	FOSSIL GROUP
Abri Pataud *	Anatomically modern *Homo sapiens* (AMHS)
Cro Magnon 3*	
Irhoud 1*	
Liujiang	
Mladec 1*	
Ohalo 2*	
Predmosti 3*	
Qafzeh 6*, 9	
Rond du Barry*	
Skhul 5	
Ziyang	
Dmanisi 2280*	Early Pleistocene
ER 3733*, 3883*	
Ngandong 1, 6, 7, 10, 11, 12	*Homo erectus (sensu stricto)*
Sangiran 2*, 17	
Sambungmacan 1, 3	
Trinil	
Zhoukoudian (ZKD) 3*, 5*, 10*	
Arago*	Middle Pleistocene
Bodo*	
Ceprano*	
Dali*	
Elandsfontein	
Florisbad	
Kabwe	
Laetoli 18*	
Maba	
Narmada	
Petralona	
Steinheim	
Zuttiyeh*	
Amud	Neandertal
Forbes Quarry	
Guattari (Monte Circeo)	
Krapina C, E*	
La Chapelle aux Saints*	
La Ferrassie*	
La Quina 5*	
Neandertal	
Shanidar 1*, 5*	
Spy 1, 2	

*casts

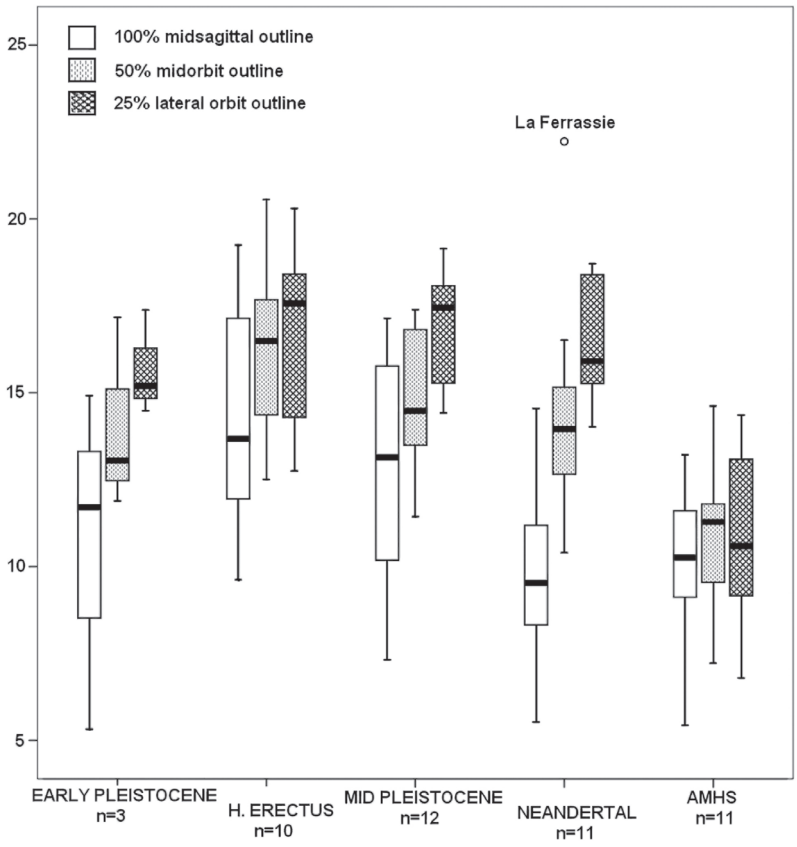

***Fig. 5 - Boxplots of browridge projection based on midsagittal (solid white), parasagittal mid-orbital (black dots) and lateral orbital (black hash lines) profiles for five groups of Pleistocene* Homo.**

H. erectus and Neandertals; and in one analysis (the size-standardized mid-orbital outline) they were significantly different from every other sample group. The differences were so consistent that, aside from anatomically modern *H. sapiens*, the Middle Pleistocene sample exhibited the most statistically distinctive frontal bone morphology in the study.

This point is relevant considering that two of the archaic retentions that Middle Pleistocene hominins are described as having are massively built supraorbital tori and flattened frontals (Rightmire, 2007). With respect to frontal flatness, these fossils were not significantly different from any group except AMHS in my measure of this trait (maximum frontal subtense), and a boxplot reveals a strong similarity with *H. erectus* in both median and range for this trait (Fig. 6). In supraorbital torus morphology, the lateral torus shows the most marked increase in projection relative to the mid-orbit for any sample in this study in terms of median values. To some extent this is due to the relatively low median value of the 50% projection measure, which aligns more with Neandertals than *H. erectus* and is influenced by the low values for Arago and Steinheim, both of which are distorted. But notably two large African specimens, Bodo and Laetoli 18, along with Dali which has also been described as having a massive supraorbital torus (Pope, 1992) also fall at the lowest end of the mid-Pleistocene *Homo* range for this trait. So while the torus of Middle Pleistocene *Homo* does appear to be

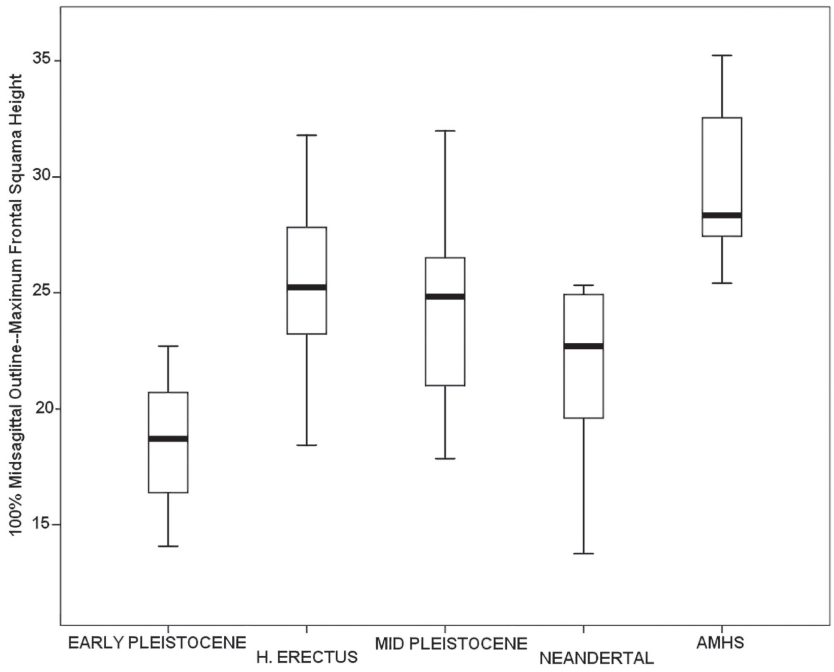

***Fig. 6 - Boxplots of maximum frontal squama projection (frontal subtense height) for five groups of Pleistocene* Homo.**

massive, the pattern that seems to really distinguish this group is the *lateral* browridge, which displays a consistent (as expressed by the limited range of variability) pattern of greatest projection in the lateral-most aspect. It bears repeating that the height of the torus in these fossils, which is notably large for many of them, is in fact so variable as to be of limited utility in characterizing this group (Rightmire, 2008) so it is more the projection of the lateral torus than its height that contributes to the distinctive nature of Middle Pleistocene *Homo* frontal bone morphology.

For the most part Neandertal frontal bone morphology is neither distinctively long nor low, despite descriptions of the overall cranium as being this way (Stringer & Gamble, 1993). Also, interestingly I did not find evidence of a glabellar fossa or depression; in fact the glabellar region of Neandertals was nearly identical in absolute prominence as well as range and median values to that of AMHS. Despite the similar absolute measurements of glabellar projection for the Neandertal and anatomically modern *Homo sapiens* samples, these two populations are rarely described as sharing this trait and indeed, while the glabellar region of Neandertals is described as "depressed" that of *H. sapiens* is sometimes referred to as "swollen" (Tattersall & Schwartz, 2008). This is partly due to the different forehead configuration of AMHS, often (but not always) rising directly up from the browridge region without a separating sulcus, along with the receding or absent lateral torus projection of this group. However, in quantitative terms it is more accurate to describe the Neandertal medial browridge as that of AMHS is described: frequently (but not universally) having a non-projecting or only slightly projecting glabellar region relative to that of the lateral browridges.

Interregional differences between European and West Asian Neandertal frontal bone morphology have been reported (Howell, 1957;

Simmons & Smith, 1991; Bruner *et al.*, 2004) and the Amud specimen has been described as being more similar to western European vs. other west Asian Neandertals (Suzuki & Takai, 1970), both of which I found as well. On the whole, the west Asian Neandertals did not form a cohesive morphotype in frontal bone morphology. While Shanidar 1 and 5 were consistently at the lower end of the range in terms of browridge projection and frontal flatness as previously reported (Trinkaus, 1983), Amud was not. The western European sample also had a high degree of variability, so much so that it is not possible to characterize their frontal bone morphology in a way that would sufficiently include all of them.

In virtually every element of frontal bone morphology studied here, the AMHS sample differed significantly in both size and size/shape analyses from all other groups. The two exceptions were glabellar morphology, in which AMHS differed significantly only from *Homo erectus* (which itself was the group with distinctive morphology relative to both Late Pleistocene samples) and frontal chord, in which the AMHS sample was not significantly different from any other—and in which only one significant difference was found at all, between the Early Pleistocene and Indonesian *H. erectus* samples.

However, within the AMHS sample there were no obvious morphological trends. While the older African/Israeli specimens did tend to express more robust morphology such as flatter frontals and more prominent brows, in many of these measures the reverse was not true: the younger Upper Paleolithic European specimens did not necessarily possess more gracile, rounded frontals. This issue is important when considered in the context of previous studies, which have used the reduction or absence of supraorbital torus as a defining trait of AMHS (Lieberman *et al.*, 2002). While this is true in general, the distinction between reduction and absence is a vague one, particularly throughout the late-Middle and early-Late Pleistocene. The ranges for Neandertals and Middle Pleistocene *Homo* overlap in several analyses. In addition, while the mean values for AMHS and other samples were, for the most part, significantly different, the ranges were overlapping as well with Neandertals, particularly in the midsagittal and 50% profiles and browridge projection values. For example, Skhul 5 misclassified as a Neandertal in both the raw and size-standardized analyses of the 50% outline; and the Irhoud 1, Skhul 5, and even the Magadlenian Rond du Barry specimens had browridge projections that overlapped with Neandertals from La Ferrassie and Gibraltar. Thus, between early AMHS and Neandertals there does not appear to be a distinctive pattern in frontal bone morphology, particularly in the browridge or midsagittal profiles, and this bone should not be used to diagnose them.

Having said that, in a statistical sense this study found AMHS to be significantly different in most respects for this aspect of the frontal bone. And in measures of lateral brow projection, AMHS was the only group that was significantly different from all other groups, indicating that these traits are diagnostic. The consistent findings of significant differences in every test are consistent with recent research demonstrating the derived nature of AMHS morphology, particularly in the craniofacial skeleton (Trinkaus, 2003, 2006). However, as stated earlier, while on average the AMHS sample is different, the range of variation both in time and space of browridge prominence within the Late Pleistocene was considerable. This makes it difficult to offer a comprehensive statement about how frontal bone morphology is patterned within early *H. sapiens* as a whole that sets it apart from other Pleistocene groups, a result also supported by previous studies (Smith *et al.*, 1989; Simmons *et al.*, 1991; Frayer *et al.*, 1993). (Smith *et al.*, 1989; Simmons *et al.*, 1991; Frayer *et al.*, 1993)

Conclusion

Based on this, what do we know about sources of variation in frontal bone morphology within the genus *Homo*? First, the biomechanical models have been explored extensively, and there is no repeatable strong evidence that

morphological variation in the supraorbital morphology of human and nonhuman primates is a plastic, *in vivo* response to high loading levels. So differences in frontal bone morphology are almost certainly not primarily a reflection of differences in activity patterns or levels among individuals (Ravosa, 1988, 1991; Lieberman, 2000) (although see: Prossinger *et al.*, 2000). Supraorbital morphology is most likely related to changing spatial relationships between the neurocranium, splanchnocranium and basicranium (Lieberman, 2000; Fiscella & Smith, 2006), as Weidenreich first suggested several decades ago (Weidenreich, 1941). Studies focusing on modern humans further support this model (Vinyard & Smith, 1997, 2001), as do those investigating the emergence and definition of modern human craniofacial form (Lieberman, 2000; Lieberman *et al.*, 2002; Tillier, 2007; Pearson, 2008).

In terms of its phylogenetic utility, while certain traits can be useful for delineating between specific sets of temporal or regional fossil samples, on the whole variation in the frontal bone is distributed among commonly recognized fossil groups in a continuous fashion. Despite previous research that has described population- and species-level differences in frontal bone morphology, the results of quantitative studies indicate that for many aspects of this bone such as supraorbital torus projection, frontal chord and frontal subtense, Pleistocene hominin populations do not differ significantly.

The notable exception to this statement is the distinctiveness of anatomically modern *H. sapiens.* Perhaps not surprisingly, this group is consistently significantly different from other Pleistocene fossil groups in aspects of frontal flatness/curvature, supraorbital torus projection, and overall sagittal and parasagittal form. The differences are related to both size and shape. However, the caveat of overlapping ranges among all archaic *Homo* groups, and between Neandertals and anatomically modern humans, means that only the lateral aspects of the frontal bone likely carry sufficient valence to differentiate between the two groups; in other respects, their ranges overlap considerably. Second, there is not necessarily a one-to-one correspondence between a character or trait and evolutionary relationships. So phylogenies that are ultimately built upon cranial studies such as this should take into consideration not just shared localized morphology but larger issues—such as character weighting, adaptive significance, and the relationship between micro- and macroevolutionary change. These and other factors are important to consider when using morphology to reconstruct the evolutionary history of our species.

Acknowledgments

I am grateful to Emiliano Bruner for the invitation to submit this review. A special thanks to José Manuel de la Cuétara for his assistance with the images. Funding for the research presented here was provided by the National Science Foundation (Grant BCS 0004139), the Wenner-Gren Foundation, the American Association of University Women, the Olin Fellowship Program at Washington University, the Department of Anthropology and the Graduate School of Arts and Sciences at Washington University, and the Department of Anthropology at Texas A&M University.

Info on the web

http://www.sciencedirect.com/science/article/pii/S0047248409001675 or
http://dx.doi.org/10.1016/j.jhevol.2009.09.003
Outlines of the frontal bones of 45 Pleistocene hominin fossils are available in the Supplemental Online Material of Athreya's 2009 Journal of Human Evolution article.

http://www.bartleby.com/107/33.html
The anatomy of the frontal bone as described in Gray's Anatomy.

http://johnhawks.net/explainer/laboratory/frontal
John Hawk's Paleoanthropology blog also contains lab exercises on frontal bone anatomy.

References

Antón S.C. 2002. Evolutionary significance of cranial variation in Asian *Homo erectus*. *Am. J. Phys. Anthropol.*, 118:301-323.

Antón S.C. 2003. Natural history of *Homo erectus*. *Yearb. Phys. Anthrop.,* 46:126-170.

Arsuaga J-L., Martínez I., Gracia A. & Lorenzo C. 1997. The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative study. *J. Hum. Evol.,* 33:219-281.

Athreya S. 2006. Patterning of geographic variation in Middle Pleistocene *Homo* frontal bone morphology. *J. Hum. Evol.,* 50:627-643.

Athreya S. 2009. A comparative study of frontal bone morphology among Pleistocene hominin fossil groups. *J. Hum. Evol.,* 57:786-804.

Barstra G. & Basoeki, 1989. Recent Work on the Pleistocene and the Palaeolithic of Java. *Curr. Anthrop.,* 30:241-244.

Barstra G., Soegondho S. & Van der Wijk A. 1988. Ngandong man: age and artefacts. *J. Hum. Evol.,* 17:325-337.

Blake C.C. 1864. On the Alleged Peculiar Characters, and Assumed Antiquity of the Human Cranium from the Neanderthal. *Journal of the Anthropological Society of London,* 2:cxxxix-clvii.

Bookstein F., Schäfer K., Prossinger H., Seidler H., Fieder M., Stringer C., Weber G.W., Arsuaga J-L., Slice D.E., Rohlf J., Recheis W., Mariam A.J. & Marcus L. 1999. Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. *Anat. Rec.,* 257:217-224.

Boule M. 1913. *L'Homme Fossile de La Chapelle-aux-Saints*. Masson, Paris.

Boule M. & Vallois H.V. 1957. *Fossil Men*. Dryden Press, New York.

Bräuer G. 1992. Africa's Place in the Evolution of *Homo sapiens*. In G. Braüer & F. Smith (eds): *Continuity or Replacement: Controversies in* Homo sapiens *Evolution*, pp. 83-97. A.A. Balkema, Rotterdam, Netherlands.

Bruner E. 2007. Cranial shape and size variation in human evolution: Structural and functional perspectives. *Child's Nervous System,* 23:1357-1365.

Bruner E. & Holloway R.L. 2010. A bivariate approach to the widening of the frontal lobes in the genus Homo. *J. Hum. Evol.,* 58:138-146.

Bruner E. & Manzi G. 2005. CT-based description and phyletic evaluation of the archaic human calvarium from Ceprano, Italy. *Anat. Rec. A,* 285:643-657.

Bruner E. & Manzi G. 2007. Landmark-based shape analysis of the archaic *Homo* calvarium from Ceprano (Italy). *Am. J. Phys. Anthropol.,* 132:355-366.

Bruner E., Saracino B., Ricci F., Tafuri M., Passarello P. & Manzi G. 2004. Midsagittal cranial shape variation in the genus *Homo* by geometric morphometrics. *Coll. Antrhopol.,* 28:99-112.

Busk G. 1861. Translation with comments of "On the Crania of the Most Ancient Races of Man" by D. Schaafhausen. *Natural History Review*, pp. 155-175.

Conroy G., Jolly C.J., Cramer D. & Kalb J.E. 1978. Newly discovered fossil hominid skull from the Afar Depression, Ethiopia. *Nature,* 276:67-70.

Cunningham D.J. 1908. The Evolution of the Eyebrow Region of the Forehead, with Special Reference to the Excessive Supraorbital Development in the Neanderthal Race. *Transactions of the Royal Society of Edinborough,* 46:283-310.

Dean D. 1993. *The Middle Pleistocene* Homo erectus/H. sapiens *Transition*: *New Evidence from Space Curve Statistics*. Ph.D. Dissertation, City University of New York, New York.

Dean D., Hublin J-J., Holloway R.L. & Ziegler R. 1998. On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany. *J. Hum. Evol.,* 34:485-508.

Dubois E. 1896. On *Pithecanthropus erectus*: A Transitional form Between Man and the Apes. *The Journal of the Anthropological Institute of Great Britain and Ireland,* 25:240-255.

Dubois E. 1937. 1. On the Fossil Human Skulls Recently Discovered in Java and *Pithecanthropus erectus*. *Man,* 37:1-7.

Endo B. 1970. Analysis of stresses around the orbit due to masseter and temporalis muscles. *J Anthropol. Soc. Nippon,* 78:251-266.

Enlow D.H. & Hans M.G. 1996. *Essentials of Facial Growth*. Saunders, Philadelphia.

Fiscella G. & Smith F.H. 2006. Ontogenetic study of the supraorbital region in modern humans: a longitudinal test of the spatial model. *Anthropol. Anz.*, 64:147-160.

Frayer D.W., Wolpoff M.H., Thorne A.G., Smith F.H. & Pope G.G. 1993. Theories of modern human origins: the paleontological test. *Amer. Anthrop.,* 95:14-50.

Freidline S.E., Gunz P., Janković I., Harvati K. & Hublin J-J. 2012. A comprehensive morphometric analysis of the frontal and zygomatic bone of the Zuttiyeh fossil from Israel. *J. Hum. Evol.,* 62:225-241.

Heim J-L. 1976. *Les Hommes Fossiles de La Ferrassie*. Masson, Paris, New York.

Hilloowala R.A. & Trent R.B. 1988. Supraorbital ridge and masticatory apparatus II: Humans (Eskimos). *Hum. Evol.,* 3:351-356.

Howell F.C. 1957. The evolutionary significance of variation and varieties of "Neanderthal" man. *The Quarterly Review of Biology,* 32:330-347.

Howells W.W. 1973. *Cranial Variation in Man: A Study by Multivariate Analysis of Patterns of Difference Among Recent Human Populations*. Papers of the Peabody Museum (67), Harvard University, Cambridge, MA.

Hublin J-J. 1987. *Les Charactéres Dérivés* d'Homo erectus: *Rélation avec l'Augmentation de la Masse Squelettique*. In G. Giacobini (ed): *Hominidae*: *Proceedings of the Second International Congress of Human Paleontology*, pp. 199-204. Jaca, Torino.

Hublin J-J. 1998. Climatic Changes, Paleogeography, and the Evolution of the Neandertals. In T. Akazawa, K. Aoki & O. Bar-Yosef (eds): *Neandertals and Modern Humans in Western Asia*, pp. 295-310. Plenum Press, New York.

Huxley T.H. 1863. On Some Fossil Remains of Man. *Evidence as to Man's Place in Nature*. Williams and Norgate, London and Edinburgh.

Hylander W., Picq P. & Johnson K. 1991. Masticatory-stress hypotheses and the supraorbital region of primates. *Am. J. Phys. Anthropol.,* 86:1-36.

Indriati E., Swisher C.C. III, Lepre C., Quinn R.L., Suriyanto R.A., Hascaryo A.T., Grün R., Feibel C.S., Pobiner B.L., Aubert M., Lees W. & Antón S.C. 2011. The age of the 20 meter Solo River terrace, Java, Indonesia and the survival of *Homo erectus* in Asia. *PLoS ONE,* 6:e21562.

Keith S.A. 1919. The differentiation of mankind into racial types. *Annual Reports of the Smithsonian Institution*, pp. 443-453.

King W. 1864. The Reputed Fossil Man of the Neanderthal. *Quarterly Journal of Science,* 1:88-97.

Lahr M.M. 1994. The Multiregional model of modern human origins: a reassessment of its morphological basis. *J. Hum. Evol.,* 26:23-56.

Lahr M.M. & Wright R.V.S. 1996. The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. *J. Hum. Evol.,* 31:157-191.

Le Gros Clark, W.E. 1955. *The Fossil Evidence for Human Evolution*. University of Chicago Press, Chicago.

Leigh S. 1992. Cranial Capacity Evolution in Homo erectus and early Homo sapiens. *Am. J. Phys. Anthropol.,* 87:1-13.

Lieberman D.E. 2000. Ontogeny, Homology and Phylogeny in the Hominid Craniofacial Skeleton. The Problem of the Browridge. In P. O'Higgins P & M. Cohn (eds): *Development, Growth and Evolution: Implications for the Study of Hominid Skeletal Evolution*, pp. 85-122. Academic Press, London.

Lieberman D.E. 1996. How and why humans grow thin skulls: Experimental evidence for systemic cortical robusticity. *Am. J. Phys. Anthropol.,* 101:217-236.

Lieberman D.E., McBratney B.M. & Krovitz G. 2002. The evolution and development of cranial form in *Homo sapiens*. *Proc. Natl. Acad. Sci. U.S.A.,* 99:1134-1139.

Lieberman D.E. 1995. Testing hypotheses about recent human evolution from skulls. *Curr. Anthropol.,* 36:159-197.

Lyell C. 1863. Post-Pliocene Period: Fossil Human Skulls of the Neanderthal and Engis Caves. *The Geological Evidences of the Antiquity of Man with*

Remarks on Theories of the Origin of Species by Variation, pp. 75-80. John Murray, London.

May R. & Sheffer D.B. 1999. Growth changes in measurements of upper facial positioning. *Am. J. Phys. Anthropol.,* 108:269-280.

Moss M.L. & Young R.W. 1960. A functional approach to caniology. *Am. J. Phys. Anthropol.,* 18:281-292.

Oyen O.J., Rice R.W. & Cannon M.S. 1979a. Browridge structure and function in extant primates and Neanderthals. *Am. J. Phys. Anthropol.,* 51:83-96.

Oyen O.J., Walker A.C. & Rice R.W. 1979b. Craniofacial growth in olive baboons (*Papio cynocephalus anubis*): Browridge formation. *Growth,* 43:174-187.

Pearson O.M. 2008. Statistical and biological definitions of "anatomically modern" humans: Suggestions for a unified approach to modern morphology. *Evol. Anthropol.,* 17:38-48.

Picq P.G. & Hylander W.L. 1989. Endo's stress analysis of the primate skull and the functional significance of the supraorbital region. *Am. J. Phys. Anthropol.,* 79:393-398.

Pope G.G. 1992. Craniofacial evidence for the origin of modern humans in China. *Yearb. Phys. Anthrop.,* 35:243-298.

Prossinger H., Bookstein F.L., Schäfer K. & Seidler H. 2000. Reemerging stress: Supraorbital torus morphology in the mid-sagittal plane? *Anat. Rec*., 261:170-172.

Prossinger H., Seidler H., Wicke L., Weaver D., Recheis W., Stringer C. & Müller G.B. 2003. Electronic removal of encrustations inside the Steinheim cranium reveals paranasal sinus features and deformations, and provides a revised endocranial volume estimate. *Anat. Rec. B. New Anat*., 273:132-142.

Ravosa M.J. 1988. Browridge development in Cercopithecidae: A test of two models. *Am. J. Phys. Anthropol.,* 76:535-555.

Ravosa M.J. 1991. Ontogenetic perspective on mechanical and nonmechanical models of primate circumorbital morphology. *Am. J. Phys. Anthropol.,* 85:95-112.

Rightmire G.P. 1985. The Tempo and Change in the Evolution of Mid-Pleistocene *Homo*. In E. Delson (ed): *Ancestors: The Hard Evidence*, pp. 255-264. Alan R. Liss, Inc., New York.

Rightmire G.P. 1990. *The Evolution of* Homo erectus*: Comparative Anatomical Studies of an Extinct Human Species*. Cambridge University Press, Cambridge.

Rightmire G.P. 2007. Later Middle Pleistocene *Homo*. In: W. Henke W & I. Tattersall (eds): *Handbook of Paleoanthropology*, pp. 1695-1715. Springer, Berlin Heidelberg.

Rightmire G.P. 2008. *Homo* in the Middle Pleistocene: Hypodigms, variation, and species recognition. *Evol. Anthropol.,* 17:8-21.

Rosas A. & Bastir M. 2002. Thin-plate spline analysis of allometry and sexual dimorphism in the human craniofacial complex. *Am. J. Phys. Anthropol.*, 117:236-245.

Rosas A, Bastir M., Martínez-Maza C., García-Tabernero A. & Lalueza-Fox C. 2006. Inquiries into Neanderthal Craniofacial Development and Evolution: "Accretion" versus "Organismic" Models. In K. Harvati K & T. Harrison (eds): *Neanderthals Revisited: New Approaches and Perspectives*, pp. 37-70. Springer, Dordrecht, Netherlands.

Ruff C., Trinkaus E. & Holliday T. 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature,* 387:173-176.

Russell M.D. 1982. Tooth eruption and browridge formation. *Am. J. Phys. Anthropol.*, 58:59-65.

Russell M.D. 1985. The supraorbital torus: "A most remarkable peculiarity" [and Comments and Replies]. *Curr. Anthrop.*, 26:337-360.

Santa Luca A.P. 1978. A re-examination of presumed Neandertal-like fossils. *J. Hum. Evol.,* 7:619-636.

Santa Luca A.P. 1980. *The Ngandong Fossil Humans: A Comparative Study of a Far Eastern* Homo erectus *Group*. Yale University Press, New Haven.

Schaafhausen D. 1861 (1858). On the crania of the most ancient races of man (from Müller's Archiv, 1858:453) with remarks on original figures, taken from a cast of the Neanderthal cranium. Translated with comments by G. Busk. *Natural History Review,* pp.155-175.

Schmerling P. 1833. *Recherches sur des ossements fossiles découverts dans les cavernes de la province de Liège*. L'Université de Liège, P-J. Collardin, Liège.

Seidler H., Falk D. Stringer C., Wilfing H., Mueller GB., Nedden Dz., Weber G.W., Reicheis W. & Arsuaga J-L. 1997. A comparative study of stereolithographically modelled skulls of Petralona and Broken Hill: Implications for future studies of middle Pleistocene hominid evolution. *J. Hum. Evol.,* 33:691-703.

Seidler H., Weber G.W. & Wilfing H. 1995. Trigonometric analysis of the human median sagittal plane and its application in reconstruction and phylogeny. *Int. J. Anthrop.,* 10:1-13.

Shea B. 1985. On aspects of skull form in African apes and orangutans, with implications for hominoid evolution. *Am. J. Phys. Anthropol.*, 68:329-342.

Shea B. 1986. On skull form and the supraorbital torus in primates. *Curr. Anthrop.,* 27:257-260.

Simmons T. 1990 *Comparative Morphometrics of the Frontal Bone in Hominids: Implications for Models of Modern Human Origins.* Ph.D. Dissertation, University of Tennessee, Knoxville.

Simmons T., Falsetti A.B. & Smith F.H. 1991. Frontal bone morphometrics of southwest Asian Pleistocene hominids. *Am. J. Phys. Anthropol.*, 20:249-269.

Simmons T. & Smith F.H. 1991. Human population relationships in the Late Pleistocene. *Curr. Anthrop.*, 32:623-627.

Smith F.H. & Ranyard G.C. 1980. Evolution of the supraorbital region in Upper Pleistocene fossil hominids from South-Central Europe. *Am. J. Phys. Anthropol.*, 53:589-610.

Smith F.H., Simek J.F. & Harrill M.S. 1989. Geographic Variation in Supraorbital Torus Reduction during the Later Pleistocene (c. 80,000-15,000 BP). In P. Mellars and C. Stringer (eds): *The Human Revolution*, pp. 172-193. Princeton University Press, Princeton.

Spitery J. 1985. Evolution de l'os frontal chez les hominides fossiles. *L'Anthropologie,* 1:63-74.

Stringer C.B. 1984. The definition of *Homo erectus* and the existence of the species in Africa and Europe. *Courier Forschungsinstitut Senckenberg,* 69:131-143.

Stringer C.B. 1985. Middle Pleistocene Hominid Variability and the Origin of Late Pleistocene Humans. In E. Delson (ed): *Ancestors: The Hard Evidence*, pp. 289-295. Alan R. Liss, Inc., New York

Stringer C.B. & Gamble C. 1993. *In Search of the Neanderthals*. Thames and Hudson, New York.

Stringer C.B., Howell F.C. & Melentis J.K. 1979. The significance of the fossil hominid skull from Petralona, Greece. *J. Archaeol. Sci.,* 6:235-253.

Suzuki H. & Takai F. (eds) 1970. *The Amud man and his cave site*. Academic Press of Japan, Tokyo.

Tattersall I. & Schwartz J.H. 2008. The morphological distinctiveness of *Homo sapiens* and its recognition in the fossil record: Clarifying the problem. *Evol. Anthropol.,* 17:49-54.

Tillier A-M. 1977. La pneumatisation du massif craniofacial chez les hommes actuels et fossiles. *Bulletins et Memoires de la Société d'Anthropologie de Paris,* 4:177-189, 287-316.

Tillier A-M. 2007. The earliest *Homo sapiens* (*sapiens*): Biological, chronological and taxonomic perspectives. *Diogenes,* 54:110-121.

Trinkaus E. 1983. *The Shanidar Neandertals*. Academic Press, New York.

Trinkaus E. 2003. Neandertal faces were not long; modern human faces are short. *Proc. Natl. Acad. Sci. U.S.A.,* 100:8142-8145.

Trinkaus E. 2006. Modern human versus Neandertal evolutionary distinctiveness. *Curr. Anthrop.,* 47:597-620.

Trinkaus E. 2011. Late Neandertals and Early Modern Humans in Europe, Population Dynamics and Paleobiology. In S. Condemi & G-C. Weniger (eds): *Continuity and Discontinuity in the Peopling of Europe*, pp. 315-329. Springer Netherlands.

Trinkaus E., Moldovan O., Milota S., Bilgar A., Sarcina L., Athreya S., Bailey S.E., Rodrigo R., Mircea G., Higham T., Ramsey C.B. & van der Plicht J. 2003. An early modern human from the Pestera cu Oase, Romania. *Proc. Natl. Acad. Sci. U.S.A.,* 100:11231-11236.

Trinkaus E. & Shipman P. 1992. *The Neandertals*. Vintage, New York.

Trinkaus E. & Svoboda J. 2006. *Early Modern Human Evolution in Central Europe:the People of Dolní Vestonice and Pavlov*. Oxford University Press, Oxford, New York.

Vallois H.V. 1954. Neandertals and Praesapiens. *Journal of the Royal Anthropological Institute of Great Britain and Ireland,* 84:111-130.

Vinyard C.J. & Smith F.H. 1997. Morphometric relationships between the supraorbital region and frontal sinus in Melanesian crania. *Homo,* 48:1-21.

Vinyard C.J. & Smith F.H. 2001. Morphometric testing of structural hypotheses of the supraorbital region in modern humans. *Z. Morphol. Anthropol.*, 83:23-41.

Weidenreich F. 1937. The Relation of *Sinanthropus pekinensis* to *Pithecanthropus, Javanthropus* and Rhodesian Man. *Journal of the Royal Anthropological Institute of Great Britain and Ireland*, 67:51-65.

Weidenreich F. 1941. The Brain and its Role in the Phylogenetic Transformation of the Human Skull. *Trans. Am. Phil. Soc.,* 31.

Weidenreich F. 1943. *The Skull of* Sinanthropus pekinensis: *A Comparative Study on a Primitive Hominind Skull*. Geological Survey of China, Pehpei, Chungking.

Weidenreich F. 1947. Facts and speculations concerning the origin of *Homo Sapiens*. *Amer. Anthrop.,* 49:187-203.

Weidenreich F. 1951. *Morphology of Solo Man*. American Museum of Natural History, New York.

White T.D. & Folkens P.A. 2000. *Human Osteology*, 2nd edn. Academic Press, San Diego.

Associate Editor, Emiliano Bruner